Photosynthetic characteristics of *Fagus sylvatica* and *Quercus robur* established for stand conversion from *Picea abies*

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A B S T R A C T

Efforts in Europe to convert Norway spruce (*Picea abies*) plantations to broadleaf or mixed broadleaf-conifer forests could be bolstered by an increased understanding of how artificial regeneration acclimates and functions under a range of Norway spruce stand conditions. We studied foliage characteristics and leaf-level photosynthesis on 7-year-old European beech (*Fagus sylvatica*) and pedunculate oak (*Quercus robur*) regeneration established in open patches and shelterwoods of a partially harvested Norway spruce plantation in southwestern Sweden. Both species exhibited morphological plasticity at the leaf level by developing leaf blades in patches with an average mass per unit area (LMA) 54% greater than of those in shelterwoods, and at the plant level by maintaining a leaf area ratio (LAR) in shelterwoods that was 78% greater than in patches. However, we observed interspecific differences in photosynthetic capacity relative to spruce canopy openness. Photosynthetic capacity (A_{1600}, net photosynthesis at a photosynthetic photon flux density of 1600 μmol photons m^{-2} s^{-1}) of beech in respect to the canopy gradient was best related to leaf mass, and declined substantially with increasing canopy openness primarily because leaf nitrogen (N) in this species decreased about 0.9 mg g^{-1} with each 10% rise in canopy openness. In contrast, A_{1600} of oak showed a weak response to mass-based N, and furthermore the percentage of N remained constant in oak leaf tissues across the canopy gradient. Therefore, oak photosynthetic capacity along the canopy gradient was best related to leaf area, and increased as the spruce canopy thinned primarily because LMA rose 8.6 g m^{-2} for each 10% increase in canopy openness. These findings support the premise that spruce stand structure regulates photosynthetic capacity of beech through processes that determine N status of this species; leaf N (mass basis) was greatest under relatively closed spruce canopies where leaves apparently acclimate by enhancing light harvesting mechanisms. Spruce stand structure regulates photosynthetic capacity of oak through processes that control LMA; LMA was greatest under open spruce canopies of high light availability where leaves apparently acclimate by enhancing CO$_2$ fixation mechanisms.

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1. Introduction

Ecologically sound and judiciously applied forest plantation systems can provide for sustainable management of forest products, allow for conservation of natural forests, catalyze rehabilitation of degraded sites, and also enhance ecosystem services such as carbon sequestration and nutrient retention (Parrotta, 1992; Ashton et al., 1997; Harrington, 1999; Sedjo, 1999; Gardiner et al., 2004; Carnus et al., 2006). Conversely, replacement of natural forests with ill conceived plantation systems can jeopardize sustainability and lead to significant degradation of

forest ecosystems (Bengtsson et al., 2000; Gamborg and Larsen, 2003; Spiecker, 2003; Carnus et al., 2006). In Europe, a large proportion of the historical temperate deciduous forest has been lost to other land uses, degraded through centuries of grazing or other cultural practices associated with settlement, or more recently replaced with intensively managed conifer plantations (Lindbladh and Bradshaw, 1998; Zerbe, 2002; Spiecker, 2003). Norway spruce (*Picea abies* L. Karst.), for example, occupies an estimated 6–7 million ha of plantations established outside of the natural range of this conifer, and the majority of these plantations are on sites that were once dominated by broadleaf or mixed broadleaf and conifer forests (von Teuffel et al., 2004).

A substantial number of Norway spruce plantations in Europe are considered economically risky and ecologically unstable bearing a high threat of damage from disturbance agents including

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wind storms, insect pests and snow (Spiecker, 2003; Mayer et al., 2005; Slodicak and Novak, 2006; Knoke et al., 2008). Furthermore, the maintenance of spruce plantations where broadleaf forest habitat once prevailed has stifled efforts to conserve or improve regional biodiversity (Nilsson, 1997; Bengtsson et al., 2000; Lindbladh et al., 2008). Because of the considerable problems associated with some of these conifer plantations, conversion from Norway spruce to stands of mixed broadleaved species is advancing quickly, particularly on publicly owned land (Hansen and Spiecker, 2004). Restoring broadleaf forests where Norway spruce plantations are proving unsuitable is believed to be prudent under the uncertainties of climate change and also a step towards increasing forest sustainability, ecological stability, biodiversity restoration and restoration of other ecosystem processes (Elmer et al., 2004; Stanturf and Madsen, 2005; Jonášová et al., 2006; Knoke et al., 2008).

There are various silvicultural approaches for converting Norway spruce stands to broadleaf or mixed broadleaf-conifer stands. Low intensity approaches rely on natural regeneration, while managers targeting particular broadleaved species typically established artificial regeneration of the desired species under a spruce shelterwood, in gaps or patches, or in larger clearcut areas of the spruce plantation (Kenk and Guehne, 2001; von Lüpke et al., 2004; Jonášová et al., 2006). The use of a shelterwood system is particularly appealing to practitioners because the residual overstory can reduce understory competition on newly established regeneration, minimize the risk of frost damage to young seedlings, provide for nutrient retention on the site, and facilitate compliance with certain forest management policy mandates (Malcolm et al., 2001; Löf et al., 2005). Apart from these benefits, application of a shelterwood system for Norway spruce conversion has not yet been refined and managing the understory light environment for desired species is a critical silvicultural challenge in this application (Hansen and Spiecker, 2004).

Recent research on sites being converted has forwarded key information on the establishment and growth of broadleaved species in the understories of spruce shelterwood stands (Löf et al., 2005, 2007; Madsen and Löf, 2005; Ammer and Mosandl, 2007). Yet, few workers have addressed physiological functioning of artificially established broadleaf species in understory environments of spruce shelterwood stands, particularly relative to stand density and the resulting understory light environment (Kazda et al., 2004). In one of few published reports on the topic, Kazda et al. (2004) concluded that mineral limitations on a nutrient poor site reduced seedling photosynthesis for three broadleaf species more so than light availability beneath the partial spruce canopy. Additional focus on how spruce shelterwood density regulates resource availability and physiological processes of regeneration under field conditions could foster the development of biologically feasible silvicultural systems that forward the advancement of sustainable forest restoration practices.

This study, conducted in southwestern Sweden, was designed to examine foliage characteristics and photosynthesis of European beech (Fagus sylvatica L.) and pedunculate oak (Quercus robur L.) regeneration raised for 7 years under two levels of overstory stem density in a Norway spruce plantation partially harvested for conversion to broadleaved species. The objective is to gain practical insight into the mechanisms of acclimation and physiological function of these two broadleaf species established in the understories of spruce stands undergoing conversion. To meet this objective, we present findings on: (1) foliage characteristics of beech and oak regeneration established under the two overstory harvest regimes; (2) leaf-level photosynthetic light response of beech and oak reproduction established under the two overstory harvest regimes; and, (3) micro-site effects of the residual spruce canopy within each harvest regime on photo-synthetic capacity of beech and oak regeneration. Additionally, we examine the influence of the residual overstory on foliar nitrogen (N) and the role of N to photosynthetic capacity of beech and oak regeneration established in the understory of the partially harvested Norway spruce plantation.

2. Methods

2.1. Study site

The study was conducted in a 46-year-old Norway spruce plantation near the community of Åkulla, which is located 20 km east of Varberg in southwestern Sweden (57°05′N, 13°04′E). The mean annual precipitation in the region is about 740 mm, and about 56% of this precipitation occurs between May and September. In 2007, the year this study was conducted, about 560 mm of precipitation was recorded between May and September. Temperatures range from a mean of -1 °C in January to a mean of 16 °C in July (SMHI, 2007). Soil on the site is a sandy till, and ground vegetation is a grass type, primarily wavy hair grass (Deschampsia flexuosa (L.) Trin.) (Hägglund and Lundmark, 1977).

2.2. Experimental design

This experiment was conducted as a component of a larger research effort designed to examine various aspects of Norway spruce stand conversion to broadleaved species in southwestern Sweden (Löf et al., 2005). In 2001, a large-scale experimental site was established for the purpose of studying broadleaf seedling survival and growth under an array of Norway spruce stand densities. The stand was delineated into 4 blocks, each containing 4 treatment plots that were partially harvested according to 1 of 4 stand density levels. In May 2001, bareroot seedlings of various broadleaved tree species were artificially established on a 1 m × 1.5 m grid in each harvesting regime. Beech seedlings planted in this experiment were 2/0 stock raised from a Häckeberga, Sweden source, and oak seedlings were 2/2 stock raised from a Polish source. The experimental area was fenced to exclude deer (Capreolus capreolus) and moose (Alces alces). A storm struck southwestern Sweden in January 2005 causing extensive windthrow of Norway spruce on the experimental site (Löf et al., 2007). However, we selected plots for this study in a portion of the experimental site that was least affected. Additional information on treatment assignments and installation, soil properties and other details relative to establishment of the large-scale experimental site were published in Löf et al. (2005, 2007).

2.3. Sampling methods

Beech and oak saplings selected for photosynthesis measurements were sampled between 14 and 20 August 2007 in 0.16-ha treatment plots (40 m × 40 m) representative of two harvesting regimes that produced two distinct spruce canopy densities. Three saplings for each species were sampled in three treatment plots that received full canopy removal–"patch harvest", and three treatment plots that received partial canopy removal–"shelter-wood harvest" (total of 18 oaks and 18 beech). Stand conditions relative to each overstory harvesting regime are noted in Table 1. The randomly selected sample plants had to be free of apparent herbivory or other damage that would influence leaf physiology. On each sample plant, one leaf from the upper third of the crown was selected for measurement of photosynthetic light response. Mature beech leaves were sampled on shoots that had completed growth for the season. Oaks on the site were actively producing a second flush, so we sampled mature leaves from the first flush on shoots exhibiting stem elongation of a second flush. Thus, the

Table 1
Stand characteristics (mean ± standard error) of a Norway spruce plantation 7 years after receiving patch harvesting and shelterwood harvesting, Åkulla, Sweden, August 2007.

Variable	Treatment	
	Patch	Shelterwood
Density[a] (spruce stems ha^{-1})	–	576 ± 44
Spruce stem diameter (cm)	–	28.9 ± 1.1
Spruce basal area (m^2 ha^{-1})	–	27.5 ± 3.5
Leaf area index (m^2 m^{-2})	0.8 ± 0.04	2.04 ± 0.09
Light availability (mol photons m^{-2} day^{-1})	35.9 ± 0.5	12.5 ± 0.9

[a] Data for stand density, stem diameter and basal area were collected using point-quarter sampling with planted oak and beech measured for photosynthesis as the sample points.

physiological activity of shoots from which oak leaves were sampled differed from the physiological activity of shoots from which beech leaves were sampled.

Photosynthetic light response was measured on the 36 sample leaves with a Ciras-2 portable photosynthesis system and an automatic leaf cuvette (PP-Systems, Haverhill, MA, USA). The evening before leaves were measured, their respective branches were covered with a black cloth bag that eliminated light and maintained moisture status of the leaf prior to measurement. Photosynthetic light response was measured by controlling light intensity on the sample leaf with a red and white LED light source, and recording CO_2 assimilation rates as they stabilized at photosynthetic photon flux densities (PPFD) of 0, 1600, 800, 400, 200, and 50 μmol photons m^{-2} s^{-1}. Sampling was typically conducted between 09:00 and 18:00. While conducting these measurements, the reference CO_2 averaged 374.9 ± 0.9 μmol mol^{-1} and leaf temperature averaged 19.9 ± 2.3 °C in the sample chamber of the cuvette.

The 36 sample leaves were harvested to quantify leaf blade area (cm^2), dry mass (g), blade mass per area (LMA, g m^{-2}), total N_a content (mg m^{-2}) and N_m concentration (mg g^{-1}) when photosynthesis measurements were complete. Leaf blades were imaged to digitally measure blade area and then were oven-dried at 70 °C. Dry leaf tissue was ball-milled to a particle size less than 250 μm prior to measuring total N_m concentration with a mass spectrometer at the Stable Isotope Laboratory, University of Georgia, USA. All above-ground tissues of sample plants were also harvested to quantify total leaf area (m^2), total leaf mass (g), total stem mass (g) and leaf area ratio (LAR, cm^2 g^{-1}) (total leaf area/above-ground biomass).

Concurrent with photosynthesis measurements, a digital camera and hemispherical lens were used to image the stand canopy above each sample plant. These canopy images, which were collected immediately above the terminal of sample plants, were processed with WinSCANOPY software (Régent Instruments Inc., Canada) to estimate leaf area index (LAI), canopy openness and the resulting light availability experienced by each sample plant.

2.4. Data analysis

Photosyn Assist software (Dundee Scientific LTD, Scotland) was used to model photosynthetic light response for each sample leaf from measured rates of CO_2 assimilation at each controlled level of PPFD. This software utilizes the function described by Prioul and Chartier (1977) to estimate key light response variables including dark respiration (R_d), light compensation point (LCP), apparent quantum yield (Φ), maximum photosynthesis at light saturation (A_{max}), saturating light intensity (LSE), and curve convexity (k). Variable estimates obtained from modeling photosynthetic light

response of each sample leaf were then subject to analysis of variance procedures to identify general treatment effects among the response variables.

Treatment effects on photosynthetic light response variables and foliage characteristics were analyzed with analysis of variance procedures for a 2 factor factorial experiment arranged in a randomized block design. The 2 experimental factors included species and overstory harvest regime, and sample observations were considered independent with 9 independent samples for each response variable in each of the four species-overstory harvest regime combinations. Thus, the ANOVA model had 5 degrees of freedom (df) (block = 2 df; species = 1 df; overstory harvest regime = 1 df; and, species × overstory harvest regime = 1 df) with 30 df in the error term. Means of significant treatment effects were separated with Duncan's Multiple Range test.

Additionally, we conducted regression analyses to explore relationships between net photosynthesis (A) for each sample leaf and independent variables specific to the sample leaf. Simple linear regression models were built with leaf N_a, N_m and canopy openness as independent variables to predict the response of A_{1600} (net photosynthesis at a PPFD of 1600 μmol photons m^{-2} s^{-1}), LMA and LAR. Because the two overstory harvest regimes resulted in distinct levels of canopy cover, canopy openness observations tended to cluster within a range for each treatment. Thus, we caution the reader against extrapolating results beyond the range of the data. Significance for all tests was determined at an alpha level of 0.05.

3. Results

3.1. Foliage characteristics

Seven years after outplanting, distinct interspecific differences were observed for several foliage characteristics of artificially established beech and oak regeneration (Table 2). As expected, beech leaf blades were smaller in area and lower in mass than oak leaf blades. Leaf blade mass of beech also remained constant across overstory harvests, while leaf blades from oak regeneration established in patches were 74% heavier than those from shelterwoods (Table 2). Oak leaf blades were 22% heavier per unit area than beech leaf blades, but both species accumulated 54% more LMA on foliage that developed in patches (Table 2). Variation in LMA across the study site was associated with the spruce overstory increasing 5.8 and 8.6 g m^{-2} for beech and oak, respectively, with each 10% increment in spruce canopy openness (Fig. 1).

Total leaf mass of saplings did not differ between species, but leaf area was greater for beech (Table 2). For both species, establishment in patches led to a 287% increase in total leaf mass and a 144% increase in total leaf area over establishment in shelterwoods (Table 2). LAR was similar for both species with lowest averages occurring in patches (Table 2). Canopy openness accounted for 60% of the variation in LAR for beech regeneration, but only 34% of the variation in LAR for oak regeneration (Fig. 2).

N_a varied by species and harvest level rising 32% in beech and 66% in oak when regeneration was established in patches rather than shelterwoods (Table 3). Leaf N_a of both species was positively associated with LMA (Fig. 3A, C) and canopy openness (Fig. 4A, C). N_a for beech rose 0.09 g m^{-2} and N_a for oak rose 0.24 g m^{-2} with each 10% increment in canopy openness.

Both species sequestered an average of 2.4% N_m in leaf blades regardless of harvesting level (Table 3). For beech leaves, N_m decreased with increasing LMA, while the analysis suggested ($p = 0.0558$) an increasing trend for oaks (Fig. 3B and D). Canopy openness accounted for about 50% of the variation we observed in beech leaf N_m which decreased nearly 0.9 mg g^{-1} for each 10% rise in canopy openness (Fig. 4B). N_m for oak showed no response to openness of the spruce canopy (Fig. 4D).

Table 2
Foliage characteristics (mean ± standard error) and above-ground biomass of beech and oak regeneration 7 years after establishment in patch harvested and shelterwood harvested areas of a Norway spruce plantation, Åkulla, Sweden, August 2007.

Variable	Patch	Shelterwood	Species Mean
Blade mass (g)			
Beech	0.20 ± 0.02 c[a]	0.13 ± 0.01 c	0.17 ± 0.01
Oak	0.61 ± 0.08 a	0.35 ± 0.04 b	0.48 ± 0.06
Treatment mean	0.41 ± 0.06	0.24 ± 0.03	
Blade area (cm^2)			
Beech	28.5 ± 1.9	28.7 ± 1.5	28.6 ± 1.2 b
Oak	71.5 ± 11.4	61.5 ± 5.5	66.5 ± 6.3 a
Treatment mean	50.0 ± 7.7 a	45.1 ± 4.8 a	
LMA (g m^{-2})			
Beech	70.8 ± 2.0	46.7 ± 2.2	58.8 ± 3.3 b
Oak	87.3 ± 3.2	55.7 ± 1.6	71.5 ± 4.2 a
Treatment mean	79.1 ± 2.7 a	51.2 ± 1.7 b	
Total leaf mass (g)			
Beech	141.3 ± 19.6	48.3 ± 6.2	94.8 ± 15.0 a
Oak	157.5 ± 39.1	28.9 ± 4.5	93.2 ± 24.6 a
Treatment mean	149.4 ± 21.3 a	38.6 ± 4.4 b	
Total leaf area (m^2)			
Beech	2.2 ± 0.3	1.2 ± 0.2	1.7 ± 0.2 a
Oak	2.2 ± 0.6	0.5 ± 0.1	1.3 ± 0.3 b
Treatment mean	2.2 ± 0.3 a	0.9 ± 0.1 b	
Above-ground mass (g)			
Beech	1060 ± 148	335 ± 45	698 ± 115 a
Oak	1009 ± 260	143 ± 24	576 ± 165 a
Treatment mean	1035 ± 145 a	237 ± 34 b	
LAR (cm^2 g^{-1})			
Beech	21.3 ± 1.4	36.9 ± 3.2	29.1 ± 2.5 a
Oak	21.4 ± 0.7	39.3 ± 2.8	30.4 ± 2.6 a
Treatment mean	21.4 ± 0.8 b	38.1 ± 2.0 a	

[a] Where species × treatment interactions are significant, treatment combination means followed by the same letter are not different. Species or treatment means followed by the same letter are not different. Blade mass species × treatment interaction ($p > f = 0.0415$); Blade area species × treatment interaction ($p > f = 0.4330$), species ($p > f < 0.0001$), treatment ($p > f = 0.4472$); LMA species × treatment interaction ($p > f = 0.1214$), species ($p > f < 0.0001$), treatment ($p > f < 0.0001$); total leaf mass species × treatment interaction ($p > f = 0.1605$), species ($p > f = 0.0640$), treatment ($p > f < 0.0001$); total leaf area species × treatment interaction ($p > f = 0.1106$), species ($p > f = 0.0024$), treatment ($p > f < 0.0001$); Above-ground mass species × treatment interaction ($p > f = 0.6041$), species ($p > f = 0.3701$), treatment ($p > f < 0.0001$); LAR species × treatment interaction ($p > f = 0.5910$), species ($p > f = 0.5632$), treatment ($p > f < 0.0001$).

3.2. Photosynthetic light response

Photosynthetic light response curves for beech and oak regeneration established in the Norway spruce plantation did not differ in convexity ($k = 0.82 ± 0.02$) ($p = 0.7791$), and showed no photoinhibition at highest PPFDs (Fig. 5). However, our findings for these species depended on whether A was analyzed relative to leaf area or dry mass (Fig. 5). Relative to leaf area, R_{d-a}, Φ_a, and A_{max-a} were similar for both species when they were established in shelterwood plots (Table 4, Fig. 5). However, beech leaves sampled in patches developed R_{d-a} and A_{max-a} rates 133% and 20% higher, respectively, than leaves sampled in shelterwoods (Table 4, Fig. 5). Oak leaves generally showed greater physiological acclimation than beech leaves with R_{d-a} averaging 250%, Φ_a averaging 16% and A_{max-a} averaging 96% higher in patches than in shelterwoods.

Results for photosynthetic light response relative to leaf dry mass were in contrast to those observed relative to leaf area (Table 4, Fig. 5). Comparing the species, oak leaves maintained a R_{d-m} 44% greater than beech leaves. For both species, R_{d-m} averaged 73% higher in patches than in shelterwoods (Table 4). Beneath shelterwoods, beech regeneration maintained a substantially
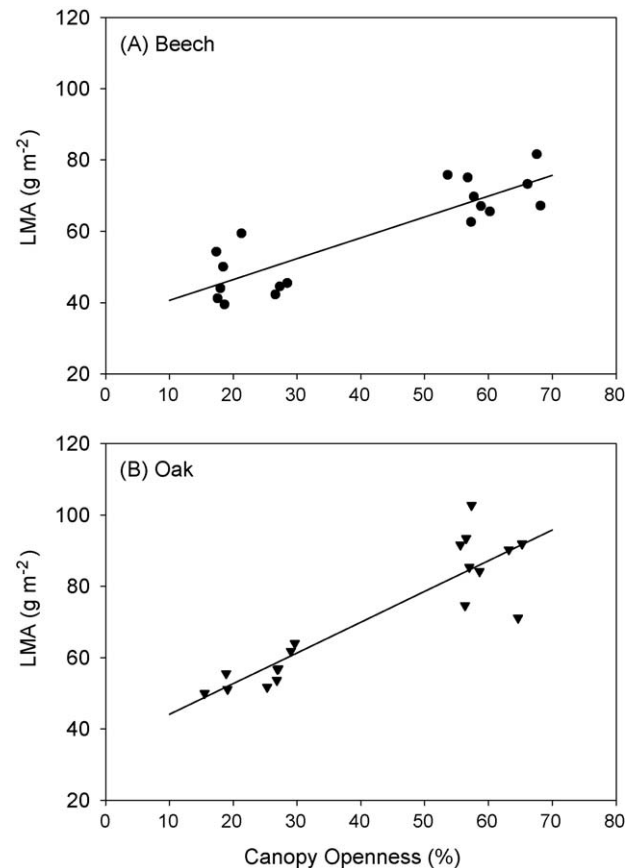

Fig. 1. Leaf blade mass per area (LMA) for beech (A) and oak (B) leaves relative to canopy openness of a Norway spruce plantation, Åkulla, Sweden. Leaves were sampled 7 years after the regeneration was established in the Norway spruce plantation. Regression statistics are: (A) beech LMA = 34.8055 + 0.5843 × openness ($p > f < 0.0001$, $r^2 = 0.7657$); (B) oak LMA = 35.4986 + 0.8615 × openness ($p > f < 0.0001$, $r^2 = 0.8050$).

higher Φ_m and A_{max-m} than oak regeneration (Table 4, Fig. 5). The Φ_m did not differ between species in patches, declining 41% for beech and 26% for oak relative to shelterwood plots (Table 4). Oak leaves that developed in patches achieved A_{max-m} rates 31 nmol CO_2 g^{-1} s^{-1} greater than those of beech, while beech leaves that developed in shelterwoods maintained A_{max-m} rates 71 nmol CO_2 g^{-1} s^{-1} greater than those of oak (Table 4).

Shifts in leaf physiology rates associated with contrasting harvesting regimes were also evident through observed changes in LCP and LSE. For both species, the LCP of leaves that developed in patches was nearly 3-fold greater than that of leaves which developed in shelterwoods (Table 4). In shelterwood understories, beech and oak leaves shared a similar estimate of light saturation. However, the LSE of oak was 17% greater than beech when regeneration was established in patches (Table 4).

3.3. Photosynthetic capacity relative to the spruce canopy

Canopy openness in the Norway spruce plantation ranged from 15 to 68% across harvest levels. It was poorly linked to the area-based photosynthetic capacity (A_{1600-a}) of beech leaves, but explained 59% of the variation we observed in mass-based photosynthetic capacity (A_{1600-m}) of this species (Fig. 6A and B). For this relationship, each 10% increment in canopy openness of the Norway spruce plantation accounted for a 16 μmol CO_2 m^{-2} s^{-1} decrease in A_{1600-m} (Fig. 6B). In contrast to our observations on beech regeneration, canopy openness was a
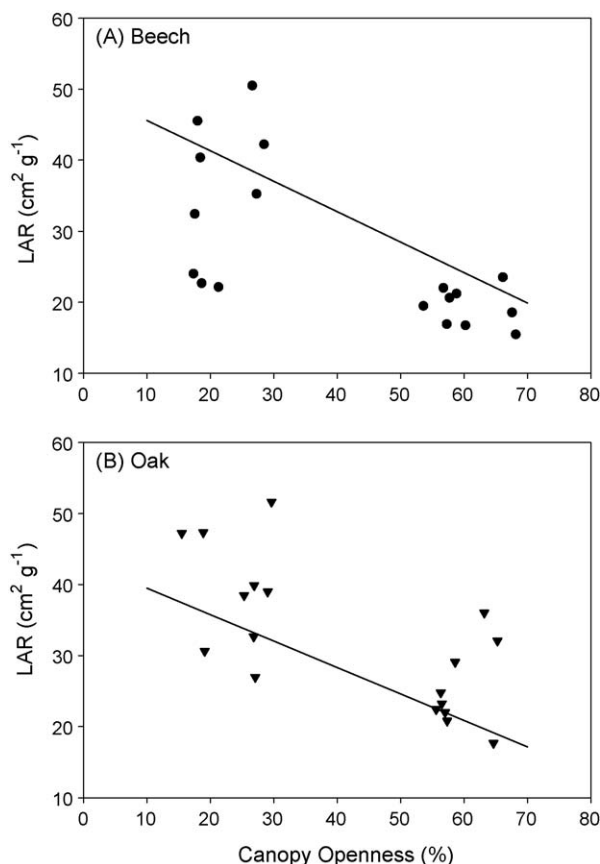
Fig. 2. Leaf area ratio (LAR = total leaf area/above-ground biomass) for beech (A) and oak (B) regeneration relative to canopy openness of a Norway spruce plantation, Åkulla, Sweden. LAR was sampled 7 years after the regeneration was established in the Norway spruce plantation. Regression statistics are: (A) beech LAR = 49.8896–0.4285 × openness ($p > f = 0.0002$, $r^2 = 0.6020$); (B) oak LAR = 43.2138–0.3725 × openness ($p > f = 0.0104$, $r^2 = 0.3448$).

Table 3
Foliar N_a content (area basis) and N_m concentration (mass basis) (mean ± standard error) of beech and oak regeneration 7 years after establishment in patch harvested and shelterwood harvested areas of a Norway spruce plantation, Åkulla, Sweden, August 2007.

Variable	Patch	Shelterwood	Species Mean
N_a (g m^{-2})			
Beech	1.58 ± 0.05 b	1.19 ± 0.06 c	1.38 ± 0.06
Oak	2.26 ± 0.15 a	1.36 ± 0.07 bc	1.81 ± 0.14
Treatment mean	1.92 ± 0.11	1.27 ± 0.05	
N_m (mg g^{-1})			
Beech	22.3 ± 0.5	25.5 ± 0.8	23.9 ± 0.6 a
Oak	25.6 ± 1.0	24.2 ± 0.8	24.9 ± 0.6 a
Treatment mean	23.9 ± 0.7 a	24.9 ± 0.6 a	

Where species × treatment interactions are significant, treatment combination means followed by the same letter are not different. Species or treatment means followed by the same letter are not different. N_a species × treatment interaction ($p > f = 0.0125$); N_m species × treatment interaction ($p > f = 0.3244$), species ($p > f = 0.2594$), treatment ($p > f = 0.6569$).

stronger driver of area-based photosynthetic capacity (A_{1600-a}) than of mass-based photosynthetic capacity (A_{1600-m}) for oak. Over 70% of the variation we observed in oak A_{1600-a} could be attributed to canopy openness, and A_{1600-a} climbed 2.2 μmol CO_2 m^{-2} s^{-1} with every 10% increment in openness of the spruce canopy (Fig. 6C). While the relationship between A_{1600-m} and canopy openness for oak was not significant ($p = 0.0588$), it was suggestive of a positive relationship between the two variables (Fig. 6D).

3.4. Photosynthetic capacity relative to leaf nitrogen

Across the study site, N_m ranged between 1.98 and 3.01% of dry leaf mass for both species (Fig. 7). For beech leaves, N_a was positively linked with A_{1600-a} explaining 34% of the variation associated with this variable. However, a stronger relationship between these variables was found relative to leaf mass such that N_m accounted for 58% of the variation in A_{1600-m} (Fig. 7B). For oak leaves, N_a was also positively related to A_{1600-a} and explained a substantial proportion of the variation we observed for this variable (Fig. 7C). In contrast to beech, A_{1600-m} for oak did not respond to variability in leaf N_m (Fig. 7D).

4. Discussion

Seven years after overstory harvesting, planted beech and oak regeneration persisted in patch harvested and shelterwood harvested areas of the Norway spruce plantation. An earlier report from this study site indicated that beech and oak seedlings maintained survival rates greater than 80% across the treated spruce plantation through year 3 (Löf et al., 2005). While their survival rates demonstrate the ability of these species to persist in the understory across a range of spruce overstory densities, growth patterns exhibited by these broadleaved species were related to the impact of spruce stand density on light availability in that beech height growth leveled above 20% light availability, while oak height growth increased with additional light availability (Löf et al., 2007). These findings were consistent with shade tolerance rankings of the species, and in agreement with other published findings on growth of beech and oak regeneration (von Lüpke, 1987; Gemmel et al., 1996; Welander and Ottosson, 1998; Löf et al., 2007). The interspecific differences in growth observed by Löf et al. (2007) prompted this investigation into the foliage characteristics and photosynthetic acclimation expressed by beech and oak regeneration under various spruce stand conditions.

4.1. Impact of silvicultural treatments on leaf morphology and acclimation

Regeneration of temperate broadleaf tree species often exhibits a strong plasticity of leaf morphology relative to light availability and/or light quality in forest understories (Abrams and Kubiske, 1990; Niinemets, 1997; Beaudet and Messier, 1998; Oguchi et al., 2006). Among the plastic traits, LMA has been recognized as an index of structural acclimation by workers studying how morphological acclimation to irradiance influences physiological function of leaves, particularly photosynthesis (Jurik, 1986; Abrams and Kubiske, 1990; Ellsworth and Reich, 1993; Niinemets and Kull, 1994; Niinemets, 1997). This plasticity of LMA to the light environment is attributed primarily to the development of mesophyll thickness and density, but may also include other structural modifications such as cuticle thickness and cell wall thickness (Ashton and Berlyn, 1994; Aranda et al., 2001; Mediavilla et al., 2001; Hanba et al., 2002; Oguchi et al., 2005). Previous research conducted on beech and oak regeneration provides substantial evidence that LMA for these species exhibits plasticity to irradiance and reacts to the prevailing light environment in a fashion similar to other temperate deciduous species. That is, leaves of both species show decreasing LMA with decreasing irradiance (Niinemets, 1997; van Hees, 1997; Aranda et al., 2001; Valladares et al., 2002; Balandier et al., 2007).

Observations of LMA in the current study are consistent with findings on beech and oak reported elsewhere (Aranda et al., 2001; Valladares et al., 2002; Balandier et al., 2007). In our study, beech and oak leaves exhibited a substantially lower LMA when regeneration was established in shelterwood harvested portions
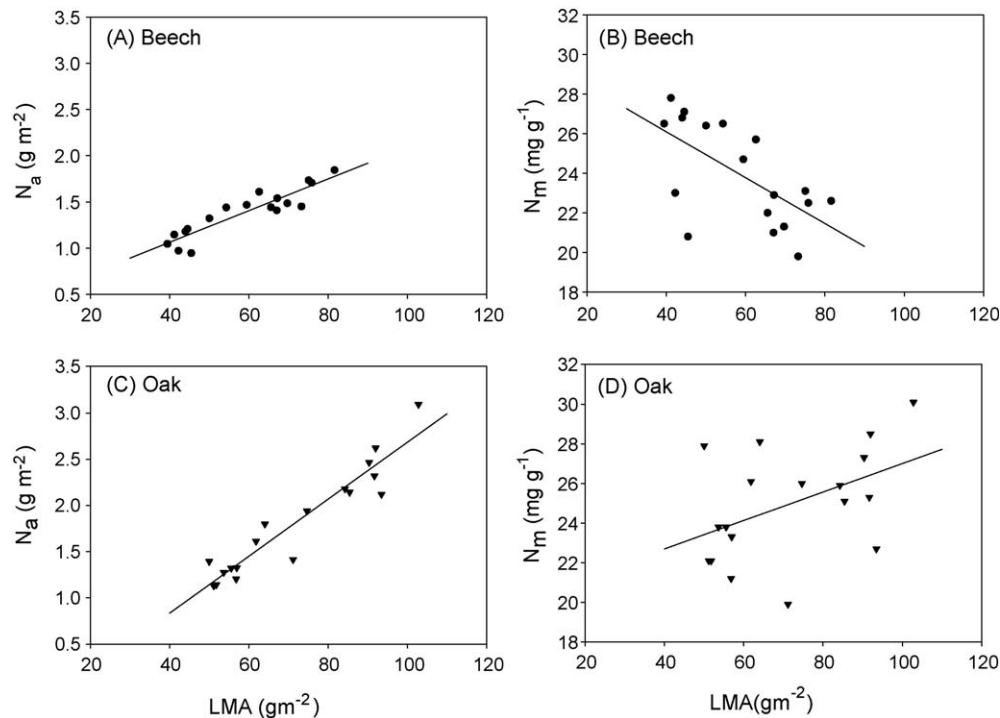
Fig. 3. N_a (area basis) and N_m (mass basis) relative to leaf blade mass per unit area (LMA) of leaves from beech and oak regeneration 7 years after establishment in a Norway spruce plantation, Åkulla, Sweden. Regression statistics are: (A) beech $N_a = 0.3781 + 0.0171 \times LMA$ ($p > f < 0.0001$, $r^2 = 0.8301$); (B) beech $N_m = 30.7240 - 0.1157 \times LMA$ ($p > f = 0.0048$, $r^2 = 0.4009$); (C) oak $N_a = -0.3999 + 0.03085 \times LMA$ ($p > f < 0.0001$, $r^2 = 0.8966$); (D) oak $N_m = 19.8199 + 0.0718 \times LMA$ ($p > f = 0.0558$, $r^2 = 0.2100$).

of the spruce stand versus patch harvested areas. This leaf-level response was closely associated with openness of the residual spruce canopy, and consistent with a gradient of understory light availability within and between harvesting treatments. A decrease in LMA with increasing spruce canopy suggests that beech and oak regeneration established in shelterwood understories developed

leaves that were acclimated to increase efficiency of light interception.

Along with morphological acclimation at the leaf level, we also observed plant-level responses in LAR that were consistent with findings reported by other workers. For temperate deciduous species including beech and oak, decreasing light availability
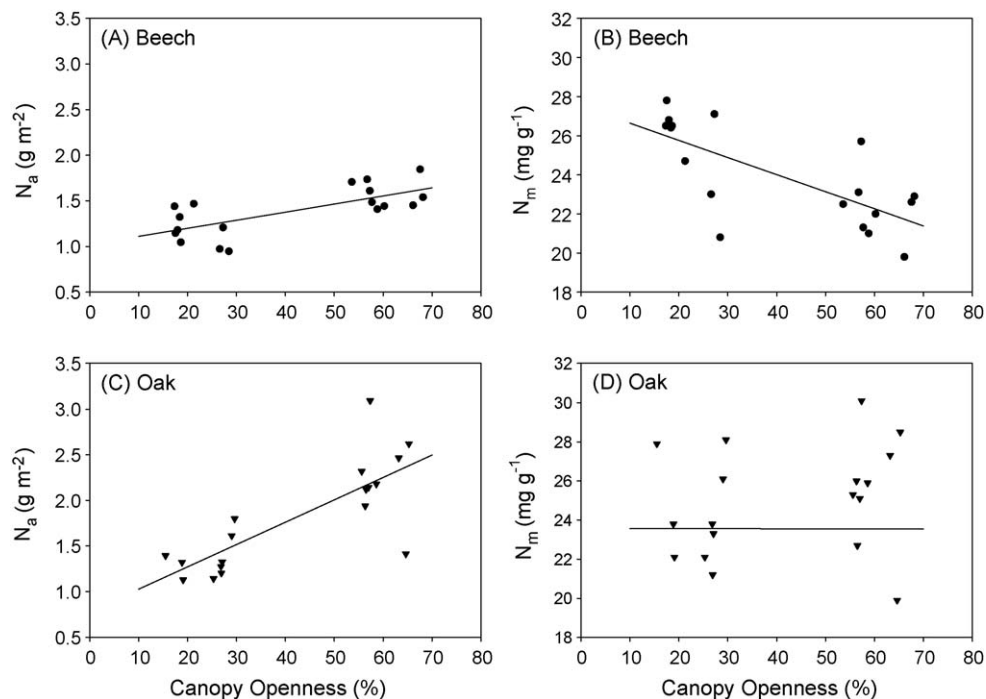

Fig. 4. N_a (area basis) and N_m (mass basis) of beech and oak leaves relative to canopy openness of a Norway spruce plantation, Åkulla, Sweden. Leaves were sampled 7 years after the regeneration was established in the Norway spruce plantation. Regression statistics are: (A) beech $N_a = 1.0214 + 0.0088 \times$ openness ($p > f = 0.0011$, $r^2 = 0.4984$); (B) beech $N_m = 27.5155 - 0.0875 \times$ openness ($p > f = 0.0008$, $r^2 = 0.5148$); (C) oak $N_a = 0.7818 + 0.0245 \times$ openness ($p > f = 0.0028$, $r^2 = 0.6136$); (D) oak $N_m = 23.4737 + 0.0354 \times$ openness ($p > f = 0.3468$, $r^2 = 0.0555$).
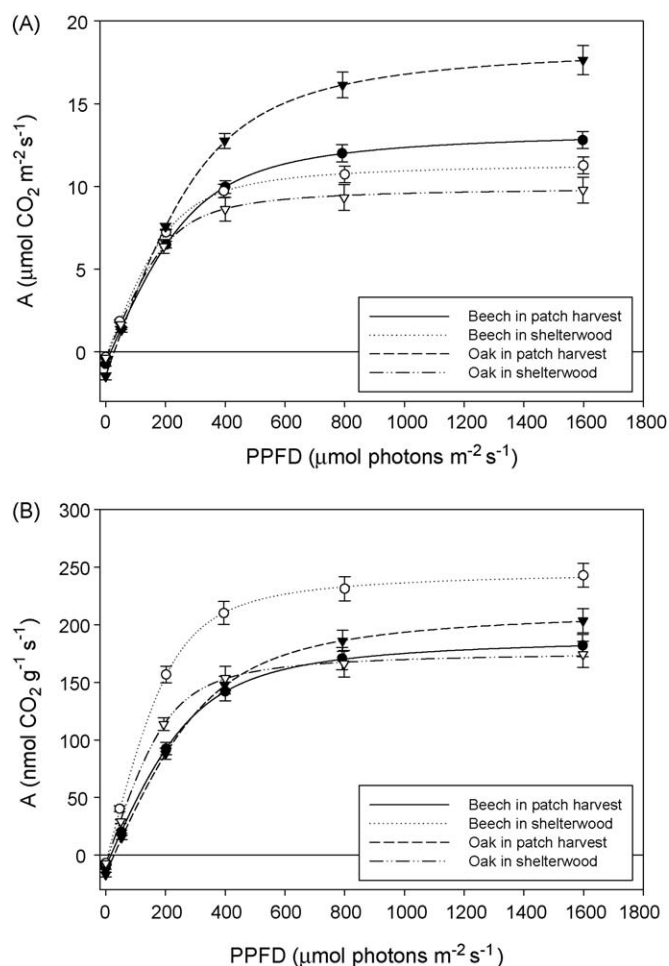
Fig. 5. Area-based (A) and mass-based (B) photosynthetic light response of beech and oak leaves sampled 7 years after regeneration was established in patch harvested and shelterwood harvested plots of a Norway spruce plantation, Åkulla, Sweden.

Table 4
Light response variables[a] for leaves of beech and oak regeneration 7 years after establishment in patch harvested and shelterwood harvested areas of a Norway spruce plantation, Åkulla, Sweden.

Variable	Patch	Shelterwood	Species mean
R_{d-a} (μmol CO_2 m^{-2} s^{-1})			
Beech	-0.7 ± 0.10 b[b]	-0.3 ± 0.06 c	-0.5 ± 0.08
Oak	-1.4 ± 0.18 a	-0.4 ± 0.07 bc	-0.9 ± 0.16
Treatment mean	-1.1 ± 0.14	-0.4 ± 0.05	
R_{d-m} (nmol CO_2 g^{-1} s^{-1})			
Beech	-10.4 ± 1.6	-6.9 ± 1.2	-8.7 ± 1.0 b
Oak	-16.5 ± 1.8	-8.6 ± 1.1	-12.5 ± 1.4 a
Treatment mean	-13.5 ± 1.4 a	-7.8 ± 0.8 b	
Φ_a (μmol CO_2 (μmol photons)$^{-1}$)			
Beech	0.042 ± 0.001 b	0.047 ± 0.001 ab	0.045 ± 0.001
Oak	0.052 ± 0.002 a	0.045 ± 0.003 b	0.049 ± 0.002
Treatment mean	0.047 ± 0.001	0.046 ± 0.001	
Φ_m (nmol CO_2 g^{-1} (μmol photons m^{-2})$^{-1}$)			
Beech	0.61 ± 0.03 c	1.04 ± 0.05 a	0.82 ± 0.06
Oak	0.61 ± 0.04 c	0.83 ± 0.06 b	0.72 ± 0.04
Treatment mean	0.61 ± 0.02	0.93 ± 0.04	
A_{max-a} (μmol CO_2 m^{-2} s^{-1})			
Beech	14.2 ± 0.55 b	11.8 ± 0.54 c	12.9 ± 0.47
Oak	20.2 ± 1.16 a	10.3 ± 0.78 c	15.2 ± 1.38
Treatment mean	17.2 ± 0.96	11.0 ± 0.50	
A_{max-m} (nmol CO_2 g^{-1} s^{-1})			
Beech	201.2 ± 10.2 bc	255.2 ± 10.6 a	228.2 ± 9.7
Oak	232.4 ± 12.2 ab	184.5 ± 11.5 c	208.5 ± 10.0
Treatment mean	216.8 ± 8.6	219.9 ± 11.4	
LCP (μmol photons m^{-2} s^{-1})			
Beech	17 ± 2.5	7 ± 1.3	12 ± 1.9 b
Oak	28 ± 3.2	10 ± 1.6	19 ± 2.8 a
Treatment mean	22 ± 2.3 a	8 ± 1.1 b	
LSE (μmol photons m^{-2} s^{-1})			
Beech	352 ± 16 b	256 ± 13 c	304 ± 16
Oak	412 ± 18 a	245 ± 21 c	329 ± 24
Treatment mean	382 ± 14	250 ± 12	

[a] R_{d-a} = dark respiration area basis, R_{d-m} = dark respiration mass basis, Φ_a = apparent quantum yield area basis, Φ_m = apparent quantum yield mass basis, A_{max-a} = maximum gross photosynthetic rate area basis, A_{max-m} = maximum gross photosynthetic rate mass basis, LCP = light compensation point, LSE = light saturation estimate.

[b] Where species × treatment interactions are significant, treatment combination means followed by the same letter are not different. Species or treatment means followed by the same letter are not different. R_{d-a} species × treatment interaction ($p > f$ = 0.0074); R_{d-m} species × treatment interaction ($p > f$ = 0.0979), species ($p > f$ = 0.0067), treatment ($p > f$ = 0.0002); Φ_a species × treatment interaction ($p > f$ = 0.0057); Φ_m species × treatment interaction ($p > f$ = 0.0205); A_{max-a} species × treatment interaction ($p > f$ < 0.0001); A_{max-m} species × treatment interaction ($p > f$ < 0.0001); LCP species × treatment interaction ($p > f$ = 0.0816), species ($p > f$ = 0.0024), treatment ($p > f$ < 0.001); LSE species × treatment interaction ($p > f$ = 0.0442).

prompts a shift in above-ground biomass distribution such that total leaf area increases relative to above-ground biomass (Walters et al., 1993; Beaudet and Messier, 1998; Valladares et al., 2002). Oak and beech regeneration studied in this experiment exhibited differing above-ground morphologies relative to the contrasting stand conditions; these morphologies were linked to canopy openness, particularly for beech. The increase in LAR with decreasing canopy openness by both broadleaf species is consistent with morphological acclimation to improve light interception in the shaded understory environments of spruce shelterwoods.

4.2. Plasticity of the photosynthetic mechanism

Photosynthetic light response curves we documented for beech and oak regeneration patterned similarly to other temperate deciduous tree species (Bazzaz and Carlson, 1982; Kubiske and Pregitzer, 1996; Kitaoka and Koike, 2005), and illustrated photosynthetic plasticity by both species relative to the understory environment created by the spruce harvests. In this respect, our findings on photosynthetic light response relative to leaf area are consistent with other reports which support the generalization that leaves of regeneration established in the understory of relatively open-canopy stands exhibit a greater R_{d-a}, A_{max-a} and LSE than those of regeneration established in the understory of relatively closed-canopy stands. Conversely, leaves acclimated to

the understory of relatively closed-canopy stands are often characterized with a lower R_{d-a}, LCP, A_{max-a} and LSE than those acclimated to relatively open forest understories (Bazzaz and Carlson, 1982; Teskey and Shrestha, 1985; Naidu and DeLucia, 1997; Oguchi et al., 2005; Balandier et al., 2007). Growth irradiance plays a key role in driving these shifts in photosynthetic light response as leaf acclimation favors CO_2 fixation in high light environments and light harvesting in low light environments (Evans, 1989; Niinemets and Tenhunen, 1997; Evans and Poorter, 2001; Kitaoka and Koike, 2005).

Photosynthetic acclimation to growth irradiance is derived from the plasticity of structural and physiological mechanisms (Ellsworth and Reich, 1992; Naidu and DeLucia, 1997; Evans and Poorter, 2001; Muraoka et al., 2003). Examination of photosynthetic light response relative to leaf mass may help distinguish interspecific difference in structural and physiological mechan-
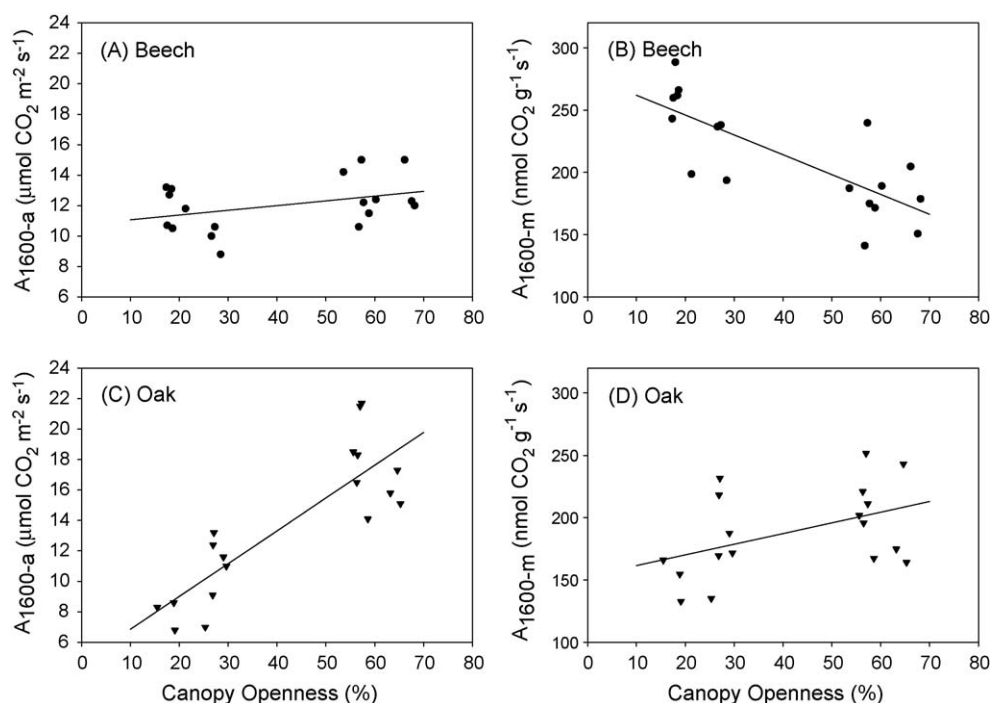
Fig. 6. Photosynthetic capacity (A_{1600}) of beech and oak leaves relative to canopy openness of a Norway spruce plantation, Åkulla, Sweden. Leaves were sampled 7 years after the regeneration was established in the Norway spruce plantation. Regression statistics are: (A) beech $A_{1600\text{-a}} = 10.7580 + 0.0310 \times$ openness ($p > f = 0.1196$, $r^2 = 0.1444$); (B) beech $A_{1600\text{-m}} = 277.8773 - 1.5932 \times$ openness ($p > f = 0.0002$, $r^2 = 0.5957$); (C) oak $A_{1600\text{-a}} = 4.7071 + 0.2152 \times$ openness ($p > f < 0.0001$, $r^2 = 0.7190$); (D) oak $A_{1600\text{-m}} = 152.9802 + 0.8566 \times$ openness ($p > f = 0.0588$, $r^2 = 0.2055$).

isms of the area-based photosynthetic acclimation described above. Compared to leaves sampled in harvested patches, beech $A_{\text{max-a}}$ declined 17% and oak $A_{\text{max-a}}$ declined 49% when leaves developed under spruce shelterwoods. Factoring in the concomitant 35% decrease in LMA, the area-based rates of A_{max} convert to a

26% increase and a 21% decrease in $A_{\text{max-m}}$ for beech and oak, respectively. For $A_{\text{max-m}}$ of beech to increase in spruce understories, this species must express substantial physiological acclimation of the photosynthetic mechanism. Following the logic of Ellsworth and Reich (1992), the net decline in $A_{\text{max-a}}$ observed for
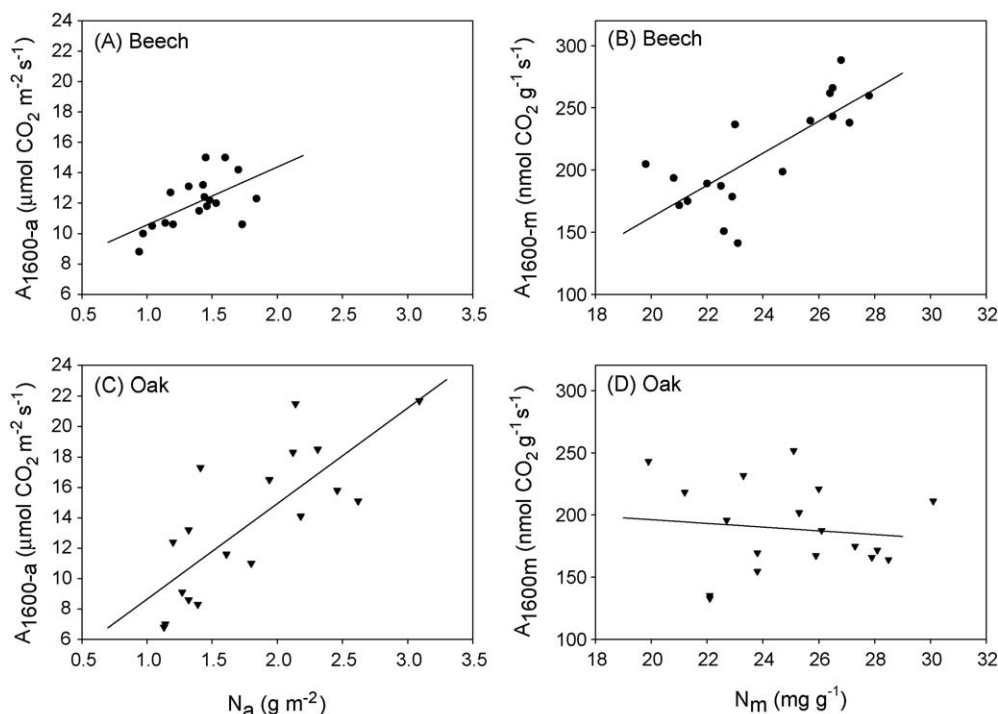

Fig. 7. Photosynthetic capacity (A_{1600}) of beech and oak leaves relative to N_a (area basis) and N_m (mass basis), Åkulla, Sweden. Leaves were sampled 7 years after the regeneration was established in the Norway spruce plantation. Regression statistics are: (A) beech $A_{1600\text{-a}} = 6.7483 + 3.8138 \times N_a$ ($p > f = 0.0105$, $r^2 = 0.3443$); (B) beech $A_{1600\text{-m}} = -95.7631 + 12.8851 \times N_m$ ($p > f = 0.0002$, $r^2 = 0.5805$); (C) oak $A_{1600\text{-a}} = 2.3547 + 6.2854 \times N_a$ ($p > f = 0.002$, $r^2 = 0.5998$); (D) oak $A_{1600\text{-m}} = 226.0398 - 1.4917 \times N_m$ ($p > f = 0.6389$, $r^2 = 0.0141$).

beech under spruce shelterwoods is indicative of a substantial decrease in photosynthesis attributable to LMA, coupled with a 26% increase in A_{max-m} derived from physiological acclimation. Conversely, 79% of the decrease in A_{max-a} for oak can be attributed to the decrease in LMA, and 21% is attributed to a net decrease in A_{max-m}. Thus, photosynthetic light responses of beech and oak indicate that these species differ in their mechanisms of photosynthetic acclimation in forest understories. While structural mechanisms of acclimation cause a net area-based decline in beech photosynthesis, its leaves compensate for some of this loss through physiological mechanisms that enhance light harvesting per unit of leaf mass. Conversely, leaf structural and physiological mechanisms contribute to the area-based down-regulation of photosynthesis by oak in the understory of spruce shelterwoods. These acclimation patterns are generally in agreement with findings by Valladares et al. (2002), who studied beech and oak raised under controlled light environments in a garden experiment. Their report provided evidence that photosynthetic plasticity of beech leaves is directed towards light harvesting mechanisms, for example, chlorophyll content $(mg\ m^{-2})$ increases with decreasing light availability (Valladares et al., 2002). This strategy is conducive to optimizing photosynthesis in relatively low light environments. In contrast, Valladares et al. (2002) reported that photosynthetic plasticity by oak leaves is directed towards carbon fixation mechanisms, for example, Rubisco activity increases with increasing light availability. This strategy is most conducive to optimizing photosynthesis in relatively high light environments.

4.3. Canopy openness, leaf nitrogen and photosynthetic capacity

While an understanding of the plastic mechanisms of photosynthetic acclimation may be academic to practitioners, identification of the environmental factors regulating photosynthetic capacity in spruce understories could be instructive for managing regeneration during stand conversion. Results from this study reveal that photosynthetic capacity (A_{1600-a}) ranged from 70% in beech to 220% in oak across understory environments in the spruce plantation. Other researchers studying photosynthetic capacity of beech or oak regeneration during stand conversion in different regions acknowledge a relationship between stand or canopy structure and photosynthetic capacity, but often derive different conclusions on which factors are driving these relationships (Aranda et al., 2004; Kazda et al., 2004; Balandier et al., 2007). Can the ranges in photosynthetic capacity observed in this study be attributed primarily to the effects of the spruce canopy on understory light environments and subsequent leaf acclimation; or, does canopy structure drive availability of other resources, such as N, that may ultimately regulate photosynthetic capacity of beech and oak in spruce stands under conversion? Findings from our research discussed below indicate that these species respond differently to environmental factors that control development of photosynthetic capacity in spruce understories.

A_{1600-a} for beech and oak leaves sampled across our study site was positively related to N_a; a finding in agreement with many other studies on these and other temperate tree species (Evans, 1989; Ellsworth and Reich, 1992; Reich et al., 1995, 1998; Aranda et al., 2004; Kitaoka and Koike, 2005; Balandier et al., 2007). Initial interpretation of this positive area-based relationship might suggest that photosynthetic capacity of beech and oak regeneration on our study site is driven by N availability. However, we also found that N_a of beech and oak leaves increased as the spruce canopy increased in openness. This positive relationship between leaf N_a and light availability in forest understories has also been documented across the temperate region (Oguchi et al., 2006; Parelle et al., 2006; Balandier et al., 2007), and is attributed to a

higher LMA often found under high light availability. Indeed, LMA of beech and oak leaves examined in this study was strongly determined by canopy openness, and N_a was strongly determined by LMA. Therefore, a conclusion that N primarily drives photosynthetic capacity of beech and oak regeneration on our study site, drawn only from the relationship between N_a and A_{1600-a}, is confounded by LMA relationships with canopy openness (Niinemets, 1997; Reich et al., 1998).

To eliminate the influence of LMA when exploring the relationship between leaf N and the development of photosynthetic capacity, it is helpful to examine the relationship on a mass basis (Niinemets, 1997). Thus, if A_{1600-m} is irresponsive to N_m it can be concluded that factors other than N availability are controlling the variability in observed photosynthetic capacity. Conversely, a positive response of A_{1600-m} to N_m would be indication that development of photosynthetic capacity to some degree is dependant on N availability.

In this study, A_{1600-m} of beech leaves increased with N_m, and N_m accounted for nearly 60% of the variation in this relationship. This is clear indication that N played an integral role in the development of photosynthetic capacity of beech regeneration on our study site. Additionally, our research indicated that N_m in beech decreased as canopy openness increased, a response that resulted in declining A_{1600-m} with increasing canopy openness. In this respect, development of photosynthetic capacity by beech hinges on N_m, and N_m is determined by canopy openness. The observation that N_m decreased with increasing canopy openness has been observed on other shade tolerant species (Niinemets, 1997) and can be attributed in part to a dilution of N_m with increasing LMA, i.e. leaves showed an altered structure which increased mass without a parallel increase in N_m (Ellsworth and Reich, 1992). Indeed, we observed a negative relationship between N_m and LMA for beech leaves in which LMA accounted for 40% of the variation in N_m. But, this also leaves a substantial proportion of the variation in N_m for beech unrelated to structural acclimation of leaves. Thus, other factors must contribute to the decline in N_m in relatively open environments. For example, it may be that the ability of beech regeneration to compete for N diminishes as shading decreases. Arguments by Kazda et al. (2004), who worked in a Norway spruce plantation in northwestern Austria, support the view that photosynthetic capacity of beech regeneration is tied to N availability in relatively open stand environments.

In contrast to beech, A_{1600-m} of oak was not responsive to N_m indicating that N did not play a primary role in the development of photosynthetic capacity of this species. Though N_a accounted for substantial variation in A_{1600-a}, N_a was determined by LMA rather than N_m for this species. N_m remained relatively constant with increasing canopy openness providing additional evidence that LMA was the primary factor driving photosynthetic capacity of oak on our study site. Thus, structural acclimation of leaves relative to light availability appears to be the primary mechanism driving photosynthetic capacity of oak regeneration along the canopy openness gradient of the spruce stand.

5. Conclusions

Morphological and physiological responses of beech and oak regeneration were examined in respect to two contrasting overstory harvesting regimes in a Norway spruce plantation under conversion to broadleaf species. For both species, regeneration established in shelterwood understories exhibited morphological acclimation of leaves that would benefit efficiency of light interception, and photosynthetic acclimation conducive to optimizing light harvesting in low light environments. Conversely, regeneration established in harvested patches displayed morphological and photosynthetic acclimation of leaves that favors CO_2

fixation in relatively high light environments. Thus, our results support the broad management premise that manipulation of spruce stand density can determine the morphology and physiology of beech and oak regeneration and in doing so will ultimately determine success of the stand conversion process.

While our findings relative to patch and shelterwood harvesting illustrate the range of beech and oak acclimation on the site, examination of how the canopy of the residual spruce stand impacted leaf morphology and physiology within and between harvest regimes provided greater insight into the mechanisms involved with acclimation. From this analysis, it was clear that beech and oak do not share the same capacity to acclimate along a gradient of canopy openness. More significantly, we observed interspecific differences in the mechanisms of morphological and physiological plasticity utilized to acclimate in understory environments.

Acclimation by beech regeneration favored photosynthesis towards the relatively closed portion of the canopy gradient in the spruce stand. Under comparatively closed canopies, beech leaves decreased LMA, but compensated for some of the lost mass by increasing N_m and exhibiting physiological plasticity that apparently enhanced light harvesting and hence photosynthetic capacity relative to leaf mass. Accordingly, photosynthetic capacity of beech regeneration established on our study site was determined by N. However, N_m for beech was clearly associated with the spruce canopy gradient, and so, N status of beech hinged on stand structure. In this respect, the photosynthetic capacity of beech was determined by N which was partitioned differently and changed in availability in response to environmental factors associated with canopy structure. Based on these findings, photosynthesis of beech regeneration would be optimized under spruce stands that receive relatively light harvests thereby creating stand conditions that favor the ability of beech to compete for N.

In contrast to beech, acclimation by oak regeneration favored photosynthesis in relatively high light environments. Photosynthetic acclimation was primarily related to plasticity of LMA, as photosynthetic capacity did not vary with N_m, and N_m in oak leaves remained constant across the spruce canopy gradient. Thus, photosynthetic capacity in oak regeneration was largely driven by light availability associated with the spruce canopy gradient. Based on these findings, greatest photosynthetic gains by oak regeneration will be achieved under management practices that maintain spruce canopies at relatively low densities.

Acknowledgements

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